RESEARCH ARTICLE

Dynamics of a coral reef community after mass mortality of branching *Acropora* corals and an outbreak of anemones

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Abstract Dynamics of a coral reef community at Tiao-Shi Reef, southern Taiwan were studied using permanent transects to examine coral recovery and successive cascades to collapse stage resulting from chronic anthropogenic impacts and typhoons. Three distinct zones were recognized within a relatively small study area (250 m across) formerly dominated by large stands of branching *Acropora* corals. The first zone still retains the dominance of branching *Acropora* corals, although they show a significant decreasing tendency. The second zone exhibits recovery with a significant increase in branching *Montipora stellata*, which is recruited and grows faster than branching *Acropora* corals. The third zone is occupied by anemone, *Condylactis* sp., and demonstrates a stable phase of coral deterioration without recovery. Such differences in coral reef community dynamics within a small spatial scale illustrate mosaic dynamics which have resulted from degradation of the water quality, patchy mortality of large branching *Acropora* thickets caused by

typhoons, the rapid asexual fragmentation and growth of *M. stellata* making it a successful colonizer, and occupation by anemone, *Condylactis* sp., together with unstable remnants of dead *Acropora* rubbles have not allowed coral recruits to survive.

Introduction

The variability of coral reef communities over different time scales has increasingly been documented (Done 1992a; Bythell et al. 1993; Connell 1997; Connell et al. 1997; Ninio et al. 2000). Disturbances such as violent storms, temperature extremes, outbreaks of predators and diseases, as well as interspecific competition tend to reduce local abundance and diversity, while recruitment and growth tend to increase them. All these processes result in complex interactions that produce a spatial–temporal mosaic of patches at different stages of recovery depending on the magnitudes and periodicities of the disturbances (Done et al. 1991; Connell et al. 1997; Done 1999; Bythell et al. 2000; Edmunds 2002). Differences among patches within a coral reef play important roles in maintaining diversity but can also result in alternative stable states (Knowlton 1992).

During the past few decades, the periodicity and severity of disturbances imposed on coral reefs have dramatically increased due to uncontrolled human activities, mainly pollution and eutrophication, over-harvesting and destructive fishing techniques, tourism development, and the contribution of international industry to exacerbation of global climate change (Rogers 1990; Hughes et al. 2003; Wilkinson 2004). These disturbances have led to mass mortality of corals and competitive overgrowth by benthic algae resulting

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in the so-called phase shifts from abundant coral to algae (Done 1992b; Hughes 1994; Hughes et al. 1999). A number of studies have revealed that sea anemones can be an alternative stage instead of algae in the phase shifts following the mortality of stony corals (Ridzwan 1993; Chadwick-Furman and Spiegel 2000; Kuguru et al. 2004).

The branching acroporid corals are known to be most vulnerable to many kinds of stresses such as storm damage, nutrient loading, diseases, thermal stress, sedimentation and invertebrate predation. Acroporids have undergone widespread decline with dramatic decrease at some localities, e.g., Looe Key, Florida and Great Barrier Reef (Miller et al. 2002; Ninio and Meekan 2002). Despite the low resistance to disturbances, fast growth rates of acroporid corals and connectivity between separate acroporid thickets due to dispersal of larvae and fragments are enabling them to recover rapidly and recolonize denuded area, thus forming large monotypic stands (Ninio and Meekan 2002). Nevertheless, chronic effects of disturbances usually exceed the regenerative capacity of corals resulting in the inability to recover over the long term (Connell 1997).

Tiao-Shi Reef is located in the northern part of Nanwan Bay, southern Taiwan (Fig. 1). Before 1992, Tiao-Shi Reef was dominated by dense thickets of branching *Acropora* spp. between the depths of 5 and 15 m (Dai 1993). For the last two decades, this reef has been influenced by overfishing, coastal development, pollution and tourism activities (Dai 1997). In addition, two strong typhoons resulted in extensive physical

damages to the branching corals in 1994 (Kao 1996). The combined effect of these disturbances have resulted in dramatic decreases in the abundance and diversity of corals (Dai et al. 1998), and since 1996 some *Acropora* rubble piles have been occupied by dense populations of the solitary sea anemone, *Condylactis* sp. (Kao 1996; Chen and Dai 2004). Thus, Tiao-Shi Reef is an ideal model of the combination of negative effects of natural and anthropogenic disturbances that have resulted in mass mortality of branching *Acropora* corals followed by a phase shift to dominance by anemones. Despite the formation of an alternative stable anemone community, some acroporid thickets still remain rather healthy and some patches composed of the dead acroporid framework exhibit initial signs of coral recovery and succession phases. The purposes of this research were to study the dynamics of the recovery and succession of the coral community within Tiao-Shi Reef and to determine the main tendency for corals in terms of their recovery and resistance to local environmental changes.

Materials and methods

Study area

The study area is located in the inner northern part of Nanwan Bay, southern Taiwan (Fig. 1). Hydrological and hydrochemical conditions of Nanwan Bay were described in detail by Dai (1991). Remarkable features of the bay are its exposure to relatively fast water flows

Fig. 1 Map and submarine profile of the study area showing locations of the study zones: *A* anemone-dominated zone, *B* coral recovery zone and *C Acropora*-dominated zone
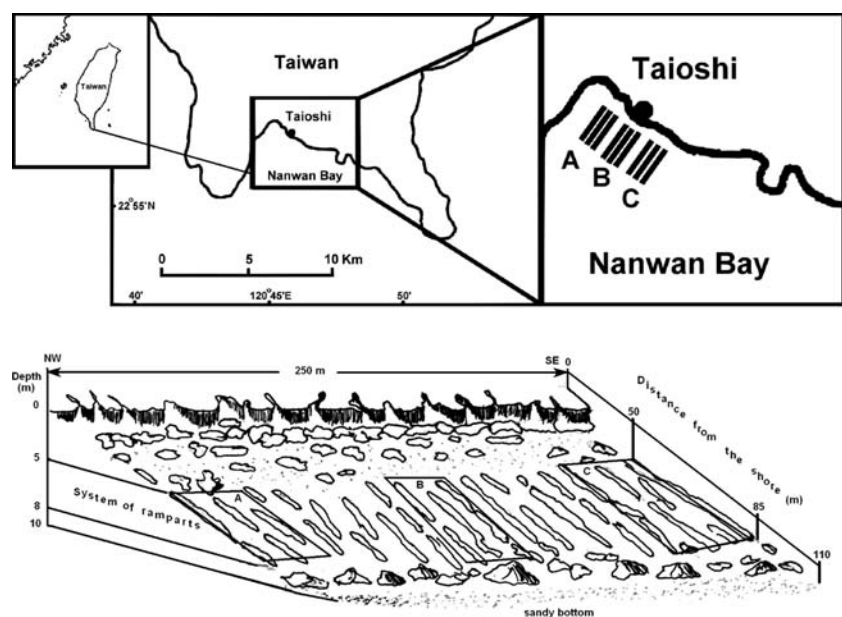
(with an average speed of 15 cm/s) caused by a branch of the strong Kuroshio current; high sedimentation rates especially in the northern part of the bay due to river discharges and heavy flooding during the rainy season [after a heavy rainfall turbidity can reach 4.3 J.T.U. (Jackson turbidity units)], and unusually high concentrations of dissolved nutrients. Nitrate during rainy season can reach 25.01 μM; nitrite to 6.08 μM; phosphate to 6.42 μM, and silicate to 52.19 μM (Dai 1991). Visibility usually does not exceed 6–7 m. The study area adjoins a large public beach with some small sources of sewage at the northwestern part of the bay. A river also discharge into southeastern part of Nanwan Bay carrying waters enriched by nutrients and pollutants into the bay within 1 km from the study area.

The area chosen for the study represents a typical spur and groove system, which characterizes the outer reef-front area of this reef. Live and dead acroporid corals are present in dense thickets, often covering the entire section of an elongated spur, and forming acroporan ramparts (Fig. 1). Ramparts begin from about 5–6 m in depth and extend down to 8 m in depth (on average) with an orientation perpendicular to the shore. In area deeper than 8 m, the spur and groove system changes into separate patches of different coral species alternating with boulders of bare limestone. This zone is rather narrow and extends down to 10 m in depth, at which point the sandy bottom gently inclines to the center of Nanwan Bay. Thus the total length of the fringing coral reef in the study area varies between 100 and 110 m, with an angle of inclination of 6–8°.

Sample design

On the basis of visual separation of ramparts according to prevailing morphological classes of benthos inhabiting the area, the study area was subdivided into three zones: *Acropora*-dominated, coral recovery and anemone-dominated zones. In each of the three zones, three transects were established for surveys. Transects were aligned perpendicular to the isobaths and directly on the ramparts. Their length varied from 15 to 20 m, depending on the rampart length. Transects were fixed and were used for periodic monitoring in April 2003, March 2004, and October 2005. Samples were taken using the photo-square method with an Olympus C-5050 underwater digital camera fixing on a tetrapod frame. Sampling frames of 0.04 m^2 (20 cm × 20 cm) in 2003 and 2004 and 0.125 m^2 (35 cm × 35 cm) in 2005 were used. A sequence of frames comprising the entire transect length was taken at each of the three transects within each study zone. Benthic categories were arranged separately in two sets: major categories and coral morphological categories. Major categories are live hard corals (LHC), anthozoans except for hard corals (ANT), macroalgae (ALG), old dead corals (mainly branching *Acropora*) covered by turf algae (DC), and sand and rubble (SR). Coral morphological categories are presented in Table 1. Cover estimation of benthic categories was performed using CPCe® (Coral Point Count with Excel extension) software developed at the National Coral Reef Institute (FL, USA). Twenty and fifty random points were used to estimate percentage cover of benthic categories within a frame sized 0.04 and 0.125 m^2, respectively. Seventy 0.04 m^2 frames and thirty 0.125 m^2 frames were randomly chosen from each transect for estimation of coverage of benthic categories. The minimal number of frames for estimation was established experimentally with a trend of mean coral cover to stabilize within the range of frames sampled.

Data analysis

Factor analysis [principal component analysis (PCA)] was used to determine relations of all species observed at the study sites to the three designed zones. Correspondence analysis (CA) was performed to ordinate the dominant species into certain zones for each year of observation. Two-way nested analysis of variance

Table 1 Coral morphological categories used in the analysis

Morphology	Code	Description
Branching *Acropora*	BA	All forms of branching *Acropora*
Branching *Montipora*	BM	*Montipora stellata*
Branching fast growing coral	BFGC	*Hydnophora rigida*
Foliaceous & laminar coral	F&LC	Correspondent forms of *Montipora, Turbinaria* and *Merulina ampliata*
Massive & encrusting coral	M&EC	*Favia, Favites, Goniastrea, Porites, Astreopora, Hydnophora* and *Millepora exaesa*
Other coral	OHC	*Pocillopora, Euphyllia, Lobophyllia, Millepora, Pavona* and *Caulastrea furcata*

(ANOVA) (with transects nested in zones) followed by post hoc Tukey HSD test was used to assess variation in categories between studied zones and to indicate transects responsible for differences found in categories within each zone. Data were tested for homogeneity of variance (Cochran C test) and were log-transformed when required [$\ln (x + 1)$]. If transformation failed to set in homogeneity of the variance, nonparametric statistics were used (Kruskall–Wallis ANOVA). Temporal variations in categories within zones were tested by one-way ANOVA for repetitive measurements or the Kruskall–Wallis test. Calculations were carried out using the STATISTICA® package (ver.6). The species richness and Shannon-Weaver diversity indices ($H = -\sum p_i \ln p_i$, where p_i is the percent cover) of each zone were also determined.

Results

Species richness and diversity

Three distinctive zones were distinguished using factor analysis which explained 96.6% of the total variance of all species observed in the study area across 3 years. The first principal component (PC) represents species variation in the *Acropora*-dominated zone; the second PC characterized species composition in the coral recovery zone and the third PC explained variations in species within the anemone-dominated zone (Table 2).

The species richness and Shannon-Weaver diversity indices increased (from 19 to 32 for species richness and from 1.91 to 2.23 for the diversity index) in the *Acropora*-dominated zone from 2003 to 2005 (Fig. 2). The coral recovery zone remained rather stable in species richness (28–32) but exhibited a decrease in species diversity index from 2.34 in 2003 to 1.98 in 2005. Both species richness and diversity

had a tendency to increase in the anemone-dominated zone (from 3 to 9 for species richness and from 0.75–0.45 to 1.23 for diversity index) but remained very low in comparison to the other study zones. In total, for the entire studied area, species richness increased from 37 species in 2003 to 44 species in 2004 and 48 species in 2005.

Distribution of common species

Distribution of abundances of common species, coverage exceeding 1% within each zone, within zones and their affinity to the distinguished zones are shown in Fig. 3. In 2003, *Acropora*-dominated zone was mostly characterized by branching *Acropora* species and the branching coral, *Hydnophora rigida*, with the prevalence of three dominant species: *Acropora intermedia* (54.6%), *Acropora formosa* (21.5%) and the anemone *Condylactis* sp. (5.5%). The coral recovery zone was mostly occupied by branching *Montipora stellata* (19.1%). The anemone-dominated zone exhibited the dominance of two species: the anemone, *Condylactis* sp. (23.8%), and the corallimorpharian, *Discosoma indosinesis* (5.5%).

In 2004, the *Acropora*-dominated zone showed little decrease in abundance of the two dominants of *A. intermedia* (51.3%) *and A. formosa* (15.2%). In the coral recovery zone, cover of *M. stellata* significantly increased from 19.1 to 46.2%. Anemone *Condylactis* sp. increased from 23.8 to 41.6% in the anemone-dominated zone.

In 2005, the abundance of *A. intermedia* decreased from 54.6% in 2003 to 41.5% in 2005 in the *Acropora*-dominated zone. The coral recovery zone was stable with only small changes in abundance of common species between the last 2 years of observation with dominance of branching *M. stellata* (45.4%). The anemone-dominated zone revealed a sharp decrease in the anemone, *Condylactis* sp., from 41.5% in 2004 to

Table 2 Factor loadings (principal component method) of evaluated percent cover of all observed species in the study area

	PC 1	PC 2	PC 3
Acropora-dominated zone 2003	**0.769**	0.476	–0.416
Acropora-dominated zone 2004	**0.780**	0.499	–0.365
Acropora-dominated zone 2005	**0.781**	0.493	–0.379
Coral recovery zone 2003	–0.610	**–0.766**	–0.190
Coral recovery zone 2004	–0.603	**–0.781**	–0.151
Coral recovery zone 2005	–0.606	**–0.778**	–0.153
Anemone-dominated zone 2003	0.203	–0.352	**0.807**
Anemone-dominated zone 2004	0.253	–0.383	**0.847**
Anemone-dominated zone 2005	0.254	–0.391	**0.874**
Total	0.343	0.327	0.296

Bold loadings are >0.7; the total is the share of components in the total factor variance
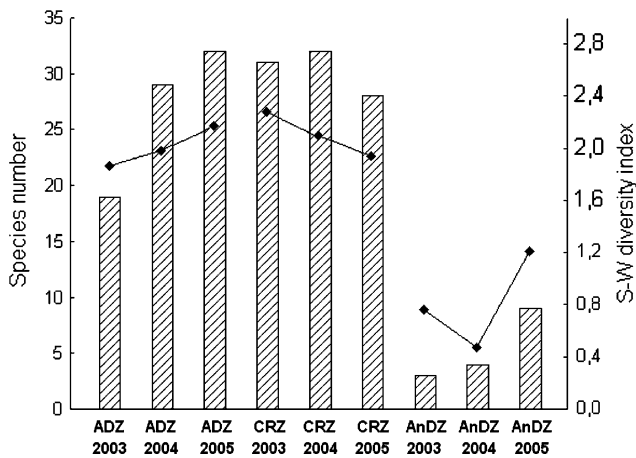
Fig. 2 Variations in species richness (left axis, *bars*) and the Shannon-Weaver diversity index (right axis, *filled rhombs*). *ADZ* *Acropora*-dominated zone, *CRZ* coral recovery zone and *AnDZ* anemone-dominated zone

16% in 2005, while the coverage of *D. indosinesis* increased from 3.9% in 2004 to 16.3% in 2005.

Spatial zonation of assigned categories

For 2 years of observation, differences between zones in categorical values remained rather stable and significant. The total coral coverage, anemone coverage, and abundance of old dead corals significantly differed between zones and transects within zones (Table 3, Fig. 4). The highest coral coverage was observed at *Acropora*-dominated zone, while anemones were found to be the most abundant in the anemone-dominated zone, which was also characterized by the largest stands of dead *Acropora* remnants. Coverage of algae as well as sand and rubble significantly varied between zones only in 2003 with the highest algal abundance in the anemone-dominated zone. However, these categories showed no differences between zones in 2004 and 2005.

Coral morphological categories were compared between *Acropora*-dominated zone and coral recovery zone, because the species number and abundance of coral in the anemone-dominated zone were very low. Coverage of branching *Acropora* and branching *Montipora* significantly differed between zones across 3 years (Table 3 and Fig. 5). Branching *Acropora* corals, mainly *A. intermedia* and *A. formosa*, were abundant in the *Acropora*-dominated zone while branching *M. stellata* dominated the coral recovery zone. Massive and encrusting coral coverage significantly differed between zones in 2003 and 2004 with higher abundance in the coral recovery zone. None of the other categories showed a significant difference between zones during the period of study.

Temporal intrazonal variations of assigned categories

Comparisons of categories between years within the same zones revealed certain dynamics in succession of the coral reef community (Figs. 4, 5). Hard coral coverage in the *Acropora*-dominated area significantly decreased from 87.2% in 2003 to 73.2% in 2005 (Fig. 4; Kruskall–Wallis test, $H = 6.2$; $P = 0.044$). In contrast, the abundance of hard corals in the coral recovery zone more than doubled from 28% in 2003 to 60% in 2005 (ANOVA, $F = 12.87$; $df = 2$; $P < 0.0001$). Temporal changes in coral coverage in the anemone-dominated zone were very small and statistically insignificant. The largest contributions to variations in coral coverage within zones were made by the two major coral morphological categories: branching *Acropora* and branching *Montipora* (Fig. 5). In the *Acropora*-dominated zone branching *Acropora* markedly decreased from 82.2% in 2003 to 66% in 2005, although these changes was not significant among the 3 years due to overlapping of their confidence levels. For a more-powerful signal to determine the tendency of reduction, 2 years (2004 and 2005) were combined into a single variable. The decrease of branching *Acropora* was significant between 2003 and the two following years (Kolmogorov–Smirnov test, $P < 0.05$; Mann–Whitney test, $P = 0.019$). A pronounced increase in coral coverage in the coral recovery zone resulted from a significant increase in the branching *Montipora* from 19.1% in 2003 to 45.4% in 2005 (ANOVA, $F = 12.1$; $df = 2$; $P = 0.0001$). No temporal variations of any of the other coral morphological categories were significant.

The abundance of anemones did not change during study period in the *Acropora*-dominated zone but was significantly higher in 2004 than in 2003 and 2005 in both the coral recovery zone (Fig. 4; Kruskall–Wallis test, $H = 10.22$; $P = 0.006$) and anemone-dominated zone (Kruskall–Wallis test; $H = 7.46$; $P = 0.023$). The main contribution in variation of anemone abundance in the coral recovery zone was made by the corallimorpharian anemone *D. bryoides*, with significantly higher coverage in 2004 (Fig. 3; Kruskall–Wallis test, $H = 11.32$; $P = 0.003$). The largest contribution to anemone variation in the anemone-dominated zone was made by the anemone, *Condylactis* sp., which exhibited significantly higher coverage in 2004 (Kruskall–Wallis test, $H = 17.89$; $P = 0.0001$). Differences in coverage of the corallimorpharian anemone, *D. indosinesis* were statistically insignificant despite a higher coverage in 2005 than the previous 2 years.
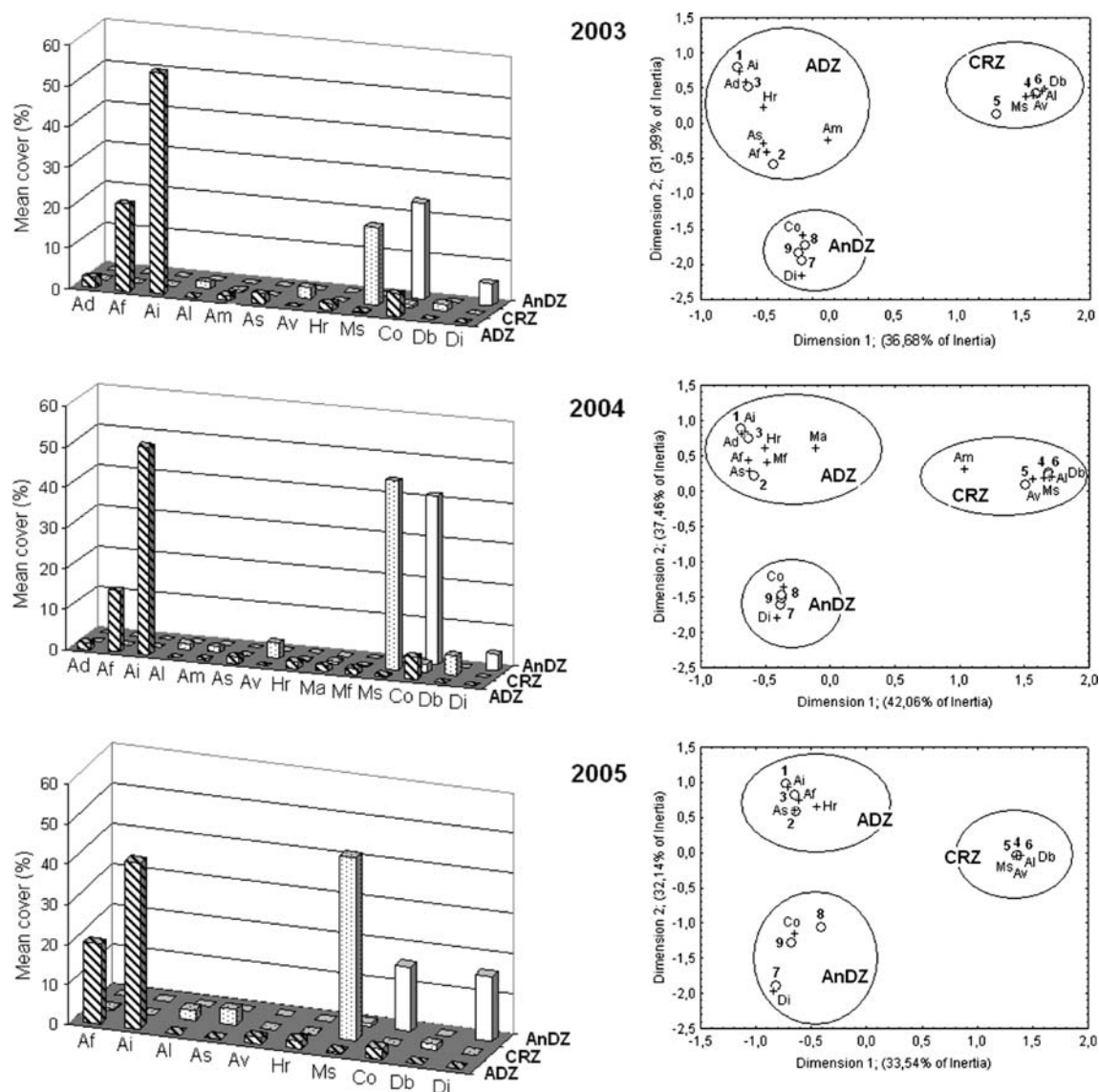
Fig. 3 *Left column* comparison of mean cover of the common species (coverage > 1%) among study zones. *Right column* results of the correspondence analysis showing the distribution of common species (+) and transects (*numbered circles*) within the study zones in the field defined by the first two correspondence factors. *ADZ Acropora*-dominated zone, *CRZ* coral recovery zone, *AnDZ* anemone-dominated zone, Ad *Acropora donei*, Af *A. formosa*, Al *A. latistella*, Am *A. microphthalma*, As *A. selago*, Av *A. valida*, Hr *Hydnophora rigida*, Ma *Montipora aequetuberculata*, Mf *M. foliosa*, Ms *M. stellata*, Co *Condylactis* sp., Db *Discosoma bryoides* and Di *D. indosinesis*

Coverage of macroalgae significantly varied in all three zones during the period of observation (Fig. 4). In the *Acropora*-dominated zone, macroalgae were more abundant in 2004 than in 2003 and 2005 (Kruskall–Wallis test, $H = 8$; $P = 0.018$). Macroalgae significantly decreased from 15.4% in 2003 to 3.7% in 2005 in the coral recovery zone (Kruskall–Wallis test, $H = 11.5$; $P = 0.003$) and also significantly decreased from 26.1% in 2003 to 0.61% in 2005 in the anemone-dominated zone (ANOVA, $F = 32.21$; $df = 2$; $P < 0.0001$).

Coverage of dead corals significantly increased from 4% in 2003 to 21.7% in 2005 in the *Acropora*-dominated zone (Kruskall–Wallis test, $H = 13.27$; $P = 0.010$) and from 40% in 2003 to 63.7% in 2005 in the anemone-dominated zone (Kruskall–Wallis test, $H = 11.14$; $P = 0.003$). In the coral recovery zone coverage of old dead coral decreased from 40.8% in 2003 to 28.2% in 2005 (Kruskall–Wallis test, $H = 7.84$; $P = 0.019$). The amount of sand and rubble did not significantly change in any zone during the 2 years.

Table 3 Summarized table of Fisher's values with the level of significance obtained by ANOVA for comparison of differences in the categories between zones within each year of observation

Category	2003		2004		2005	
	F	P	F	P	F	P
LHC	231.89	<0.0001	162.6	<0.0001	66.52	<0.0001
ANT	23.08	<0.0001	70.28	<0.0001	36.46	<0.0001
ALG	11.47	0.0001		n.s.		n.s.
DC	41.02	<0.0001	41.63	<0.0001	15.18	<0.0001
SR	6.56	0.004		n.s.		n.s.
BA	356.4	<0.0001	101.38	<0.0001	211.57	0.0001
BM	44.45	<0.0001	44.45	<0.0001	40.24	<0.0001
M&EC	6.93	0.014	6.81	0.016		n.s.

LHC living coral coverage, *ANT* anthozoans except for hard corals, *ALG* macroalgae, *DC* dead coral, *SR* sand and rubbles, *BA* branching *Acropora*, *BM* branching *Montipora*, *M&EC* massive and encrusting corals

Discussion

Dynamics across 3 years of the Tiao-Shi coral reef community demonstrate two opposite phenomena: development of recovery expressed by the rapid increases in the branching hard coral, *M. stellata*, in the coral recovery zone and a dramatic phase shift to long-term dominance by anemones with almost no coral recovery in the adjacent anemone-dominated zone. The *Acropora*-dominated zone is showing certain signs of continuous reduction in coral coverage and elimination of branching *Acropora* corals, while the total diversity has increased in this zone due to a decrease of the monotypic *Acropora* populations and increases of massive and encrusting corals.

The uniqueness of the Tiao-Shi Reef lies in the simultaneous presentation of dense thickets of *Acropora* spp., the recovery of the coral community with rapid increase of *M. stellata*, and a phase shift to the dominance by sea anemones within a small area of only 250 m across. Such a phenomenon can be considered ''mosaic dynamics'' of an individual coral reef community. Bythell et al. (2000) reported that local coral reef community dynamics were highly variable with sites that were destroyed by disease showing little or no recovery, while sites less than a kilometer away that were devastated by a hurricane were recovering well. Edmunds (2002) documented that dynamics of coral reef community on a kilometer-wide scale varied markedly and created a heterogenic mosaic of habitats. Thus, coral reefs may be composed of a mosaic of patches at different developmental stages, and individual patches often follow disparate trajectories that are determined by the combined effects of local and regional processes as well as historical effects (Done et al. 1991; Connell et al. 1997; Bythell et al. 2000; Edmunds 2002).

Several potential explanations exist for the process of the shift from the original community dominated by branching *Acropora* to the three distinct zones: (1) long-term water quality degradation with increasing sedimentation and nutrient loadings; (2) physical damage caused by typhoons being patchy at small spatial scales; (3) an outbreak of the anemone, *Condylactis* sp.; and (4) successful colonization by *M. stellata*, with slender, branching morphology and rapid regeneration and growth rates.

The dramatic changes in some areas of the reef and extinction of thickets of branching *Acropora* corals can be attributed to typhoons and significant long-term environmental changes in Nanwan Bay over the last two decades (Kao 1996; Dai 1997; Dai et al. 1998; Chen and Dai 2004; Tsai et al. 2005). Many nearshore reefs are characterized by turbid water, high abundances of fleshy macroalgae, and low abundances of corals and herbivorous fishes. Tsai et al. (2005) reported that Tiao-Shi Reef has become a highly eutrophic coral reef with dissolved inorganic nitrogen, NO_3^-, NO_2^-, NH_4^+ reaching 18.80, 12.33, 1.33, and 12.45 μM, respectively. Increases in algal abundances as a response to high nutrient inputs and overfishing in the studied area have been reported (Dai 1997; Dai et al. 1998; Hwang et al. 2004; Tsai et al. 2005) and occasionally have been recorded at Tiao-Shi Reef as occurred in 2003 in the present study, when turf algae and fleshy macroalgae were even found to be overgrowing the main dominant anemone, *Condylactis* sp., by covering the upper surfaces of the ramparts and leaving anemones beneath among the debris of old coral skeletons.

Several typhoons pass through southern Taiwan annually (Dai 1991). Two strong typhoons resulted in extensive physical damages to branching *Acropora* corals and the formation of rubble fields at Tiao-Shi Reef in August 1994 (Kao 1996). However, typhoon-

Fig. 4 Dynamics of major categories in the study zones (categories are presented in percent cover ± SE). *LHC* live hard corals, *ANT* anthozoans, *ALG* macroalgae, *DC* old dead corals (*Acropora* remnants), *SR* sand and rubble. Significant differences between transects within zones (Tukey HSD test) are marked by an *asterisk*
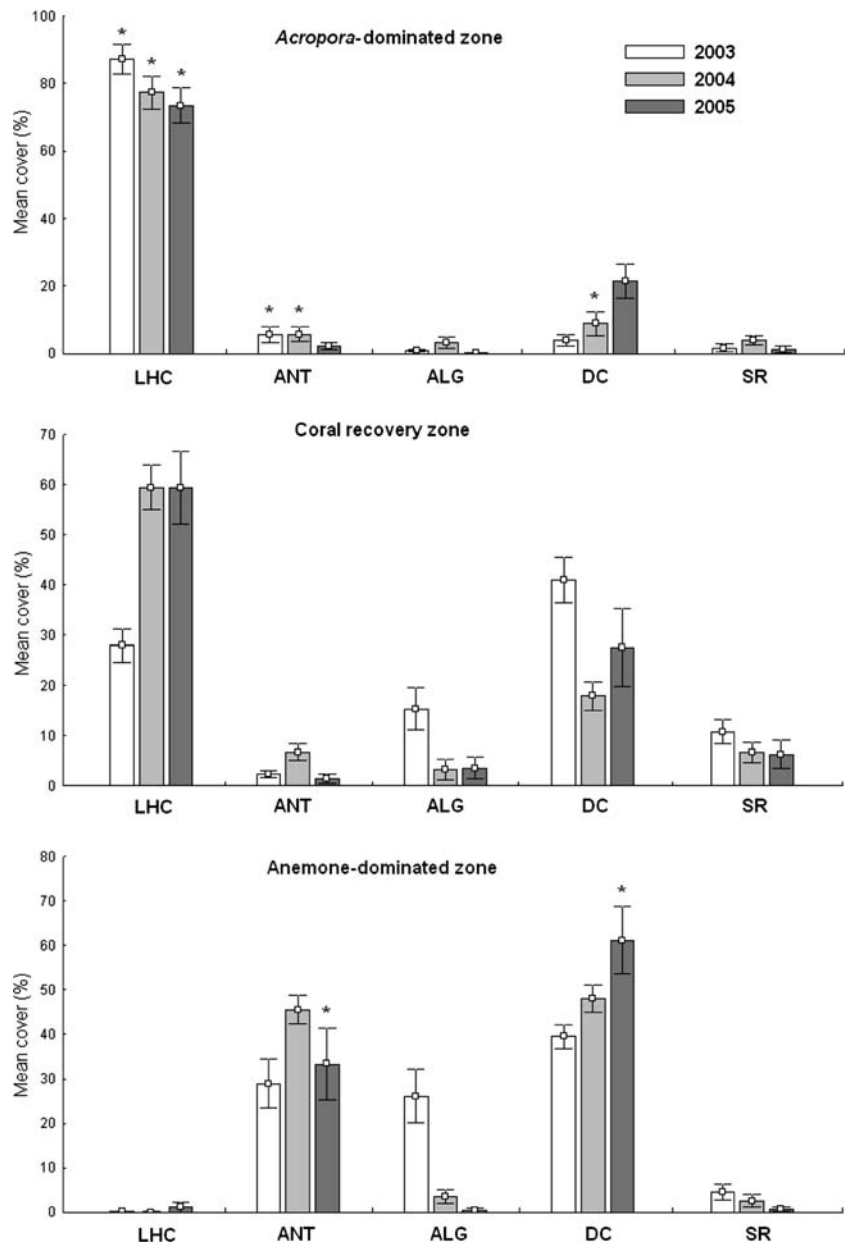

generated damage was variable among the *Acropora* patches with some remaining unchanged, some being damaged but recovering rapidly, while some thickets of dead *Acropora* rubble fields were occupied by dense populations of the sea anemone, *Condylactis* sp., since 1996 (Kao 1996). The effects of typhoon-generated physical disturbances were patchy and variable in their spatial distribution (Rogers 1992; Lirman et al. 2001). Generally, the abundant, fragile, fast-growing, branching coral species are the most susceptible to physical damage.

The causes of the anemone *Condylactis* sp. outbreak are not clear, but are likely connected to significant environmental changes including eutrophication and

sedimentation (Dai et al. 1998; Chen and Dai 2004). In addition, the intensive asexual reproduction of the sp. by longitudinal fission has likely contributed to the formation and maintenance of the dense populations (Tsai et al. 2002). Several studies have reported anemones becoming an alternate dominant to stony corals on coral reefs. The corallimorpharian anemones, *Discosoma dawydoffi* and *Discosoma howesii*, were found to dominate the reef slopes of the Pulau islands in Malaysia, where both species colonized the collapsed, dead coral branches (mostly branching *Acropora* spp.) and coral rubble forming extensive beds of contiguous aggregations (Ridzwan 1993). Chadwick-Furman and Spiegel (2000) described the

Fig. 5 Dynamics of coral morphological categories in the study zones (categories are presented in percent cover ± SE). Explanations of categories are given in Table 1. Significant differences between transects within zones (Tukey HSD test) are marked by an *asterisk*
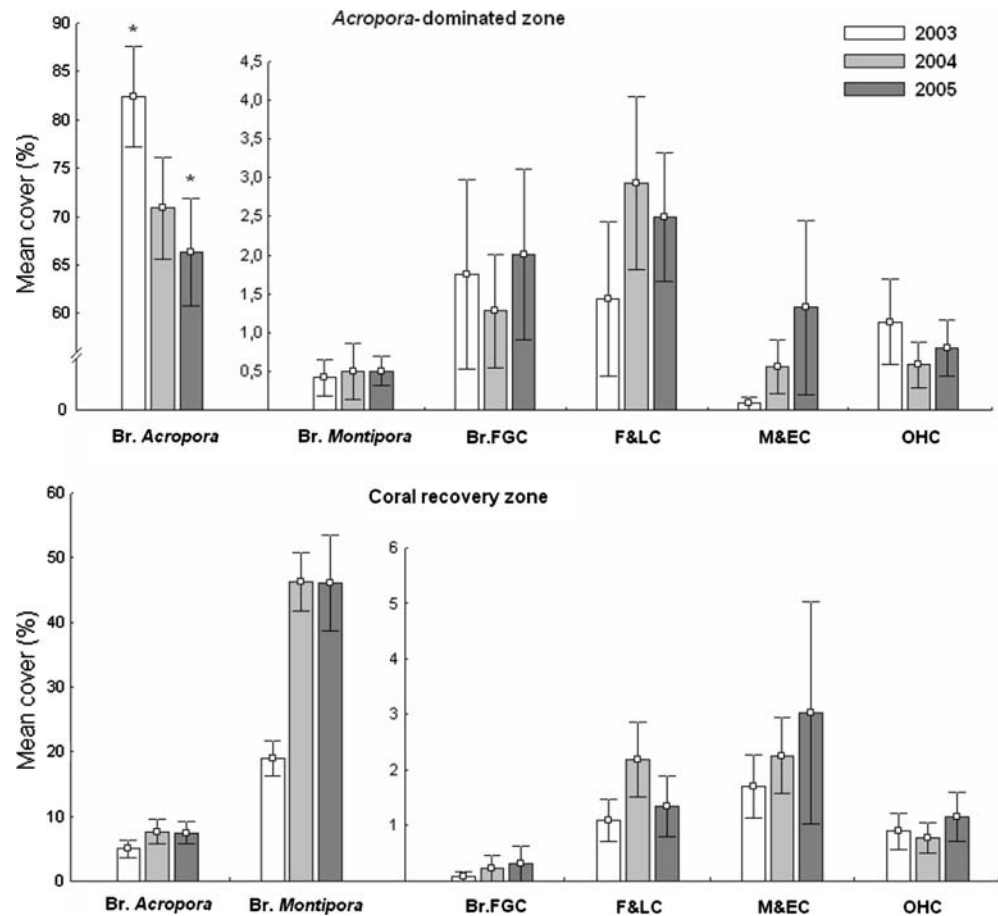
corallimorpharian *Rhodactis rhodostoma* rapidly monopolized patches formerly occupied by stony corals but which became bare substrate after a catastrophic low tide on a tropical reef in the Red Sea. Kuguru et al. (2004) described the growth and development of dense populations of the corallimorpharian, *R. rhodostoma*, that outcompeted corals for space; this was attributed to the increased nutrient content on Tanzanian reefs.

The anemone-dominated zone exhibits a stable stage of collapse in coral development. There is the appearance of coral recruits and small colonies, but so far, they have been ephemeral and insignificant. It is proposed that occupation by anemones together with unstable remnants of dead *Acropora* rubble have not allowed coral recruits to survive. Fox et al. (2003) found that rubble movement was detrimental to small stony corals, especially in high-current areas. In addition, rubble overgrown by anemones and corallimorpharians inhibited hard coral survival and stabilized the alternate state.

The pronounced development of *M. stellata* is related to its rapid regeneration and growth rates as well

as the initial large numbers of this species around and within the acroporid ramparts in the coral recovery zone (Fan, unpublished data). After extinction of the *Acropora* corals, fast asexual growth, fragmentation, and recruits contributed to the successive development of pure populations of branching *M. stellata*. In addition, dense aggregations of *M. stellata* in the coral recovery zone did not allow *Condylactis* sp. to occupy places between coral colonies, which resulted in stability of the coral growing in the zone. Kayanne et al. (2002) monitored coral recovery in the Ryukyu Islands and found that branching *Montipora* had a high potential for recovery after mortality due to its fast growth rates, and the extent of recovery was correlated with patch size.

The general trend occurring at Tiao-Shi Reef is elimination of branching *Acropora* corals and a shift to dominance by coral species of branching *M. stellata* and those more tolerant of high sedimentation and eutrophication such as massive and encrusting corals. Our results demonstrate that in some cases, coral reef communities are unable to recover naturally despite adjacent sources of recruits. The different responses of

the three zones studied within such a small spatial scale suggest that mosaic dynamics are occurring in this coral reef community.

References

Bythell JC, Bythell M, Cladfelter EH (1993) Initial results of a long-term coral reef monitoring program: impact of hurricane Hugo at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. J Exp Mar Biol Ecol 172:171–183

Bythell JC, Hillis-Starr ZM, Rogers CS (2000) Local variability but landscape stability in coral reef communities following repeated hurricane impacts. Mar Ecol Prog Ser 204:93–100

Chadwick-Furman NE, Spiegel M (2000) Abundance and clonal replication in the tropical corallimorpharian *Rhodactis rhodostoma*. Invert Biol 119:351–360

Chen CA, Dai CF (2004) Local phase shift from *Acropora*-dominant to *Condylactis*-dominant community in the Tiao-Shi reef, Kenting National Park, southern Taiwan. Coral Reefs 23:508

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16:101–113

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

Dai CF (1991) Reef environment and coral fauna of southern Taiwan. Atoll Res Bull 354:1–28

Dai CF (1993) Patterns of coral distribution and benthic space partitioning on the fringing reefs of southern Taiwan. Mar Ecol 42:185–204

Dai CF (1997) Assessment of present health of coral reefs in Taiwan. In: Grigg RW, Birkeland C (eds) Status of coral reefs in the Pacific. University of Hawaii, Honolulu, pp 123–131

Dai CF, Kao KM, Chen YT, Chaun ST (1998) Changes of coral communities in the Nan-wan Bay, Kenting National Park from 1987 to 1997. Bull Natl Park 8:79–99 (in Chinese)

Done TJ (1992a) Constancy and change in some Great Barrier Reef coral communities: 1980–1990. Am Zool 32:655–662

Done TJ (1992b) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132

Done TJ (1999) Coral community adaptability to environmental change at the scale of regions, reefs and reef zones. Am Zool 39:66–79

Done TJ, Dayton PK, Dayton AE, Steger R (1991) Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. Coral Reefs 9:183–192

Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs 21:357–367

Fox HE, Pet JS, Dahuri R, Caldwell RL (2003) Recovery in rubble fields: long-term impacts of blast fishing. Mar Pollut Bull 46:1024–1031

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes TP, Szmant AM, Steneck RS, Carpenter RC, Miller S (1999) Algal blooms on coral reefs: what are the causes? Limnol Oceanogr 44:1583–1586

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts and the resilience of coral reefs. Science 301:929–933

Hwang RL, Tsai CC, Lee TM (2004) Assessment of temperature and nutrient limitation on seasonal dynamics among species of *Sargassum* from a coral reef in southern Taiwan. J Phycol 40: 463–473

Kao KM (1996) The physical damage and recovery of coral communities in Kenting National Park. Research report no. 27, Kenting National Park Headquarters, Taiwan, 36 pp (in Chinese)

Kayanne H, Harii S, Ide Y, Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. Mar Ecol Prog Ser 239:93–103

Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. Am Zool 32:674–682

Kuguru BL, Mgaya YD, Öhman MC, Wagner GM (2004) The reef environment and competitive success in the Corallimorpharia. Mar Biol 145:875–884

Lirman D, Glynn PW, Baker AC, Morales GEL (2001) Combined effects of three sequential storms on the Huatulco coral reef tract, Mexico. Bull Mar Sci 69:267–278

Miller MW, Bourque AS, Bohnsack JA (2002) An analysis of the loss of acroporid corals at Looe Key, Florida, USA: 1983–2000. Coral Reefs 21:179–182

Ninio R, Meekan MG (2002) Spatial patterns in benthic communities and the dynamics of mosaic ecosystem on the Great Barrier Reef, Australia. Coral Reefs 21:95–103

Ninio R, Meekan M, Done T, Sweatman H (2000) Temporal patterns in coral assemblages on the Great Barrier Reef from local to large spatial scales. Mar Ecol Prog Ser 195:65–74

Ridzwan AR (1993) Recovery processes of coral communities following the crown-of-thorns starfish, *Acanthaster planci*, infestations of the east coast islands of Peninsular Malaysia. PhD thesis, University of Newcastle upon Tyne, Newcastle, UK

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202

Rogers CS (1992) A matter of scale: damage from Hurricane Hugo (1989) to U.S. Virgin Islands reefs at the colony, community, and whole reef level. In: Proceedings of the 7th international coral reef symposium, Guam, vol 1. pp 127–133

Tsai WH, Dai CF, Fan TY (2002) Population structure and reproduction of the sea anemone *Condylactis* sp. in Nanwan Bay, southern Taiwan. In: Proceedings of ther IUCN/WCPA-EA-4 conference, Taipei, pp 18–23

Tsai CC, Chang JS, Sheu F, Shyu YT, Yu AYC, Wong SL, Dai CF, Lee TM (2005) Seasonal growth dynamics of *Laurencia papillosa* and *Gracilaria coronopifolia* from a highly eutrophic reef in southern Taiwan: temperature limitation and nutrient availability. J Exp Mar Biol Ecol 315:49–69

Wilkinson C (2004) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville